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INTRA- AND INTERVARIETY CROSSES OF

MEDICAGO SATIVA L. AND MEDICAGO FALCATA L.

by

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INTRODUCTION

Heterosis has been found and utilized in many crop plants. Hybrid corn is a well known example. Alfalfa, another cross-fertilizing species, also is known to exhibit heterosis but its exploitation has been much less spectacular than that in corn.

Due to its autotetraploid genetic structure, alfalfa should, theoretically, show a slower rate of inbreeding depression than diploid corn. Experimental evidence has shown, however, that actual inbreeding depression in alfalfa is more rapid than that expected. Since heterosis from outcrossing is essentially the converse of inbreeding depression, the greater the sensitivity of a species to inbreeding the greater heterotic effect is expected. Therefore, hybrid alfalfa would be expected to exhibit more heterosis than hybrid corn. While this expectation has not as yet been realized, it is recognized that a direct comparison of heterosis in alfalfa and corn is difficult to make. All alfalfa plants used in breeding programs are heterozygous and no true-breeding inbred lines are available. Thus, it is difficult to establish a comparable base from which heterosis can be measured.

Dudley (1964) suggested that maximum heterosis might be obtained in single crosses made from heterozygous S_0 plants. Diversity of germ plasm also has been found important in obtaining heterosis. It is of interest to determine what kind of population and what degree of diversity of parent plants should be used in crossing in order to obtain more hybrid vigor.

In the present study, three alfalfa varieties, Alfa, Vernal, and

Kuban, were used. These varieties are different in germ plasm as well as in population structure. Crosses between varieties and within varieties were made. The primary objectives were (1) to determine what cross combinations exhibited great heterotic effect, (2) to study general and specific combining ability relationships among the progeny of these crosses, and (3) to compare self-fertility of F_1 progenies to that of their corresponding parent plants.

REVIEW OF LITERATURE

A considerable number of studies have demonstrated that alfalfa is a naturally cross-pollinated species, thus a reasonable level of vigor and fertility is maintained. Inbreeding imposed upon a population has been found to cause a rapid decrease in vegetative vigor and a marked decrease in seed yield. Kirk (1927, 1932) found, on the average, a pronounced and progressive reduction in vegetative vigor and seed yield for each generation of selfing. Similarly, Williams (1931) found that the average seed yield from S_1 plants was only 12.4 percent of that of the parent plants from which they were derived.

Sandal (1946) reported that average forage yield of 13 S_1 progenies was 31.8 percent less than the yield of the S_0 progenies derived from the same parental clones. Tysdal, _et al_.(1942) found that the forage yield of 54 S_1 lines was only 68 percent of the parental open-pollinated varieties. Inbreeding was continued for seven additional generations. In the S_8 generation, the forage yield of the 4 remaining lines was only 28 percent of the parental open-pollinated varieties. Similar reductions in forage yield have been observed by Koffman (1959), McAllister (1950), and Wilsie (1958).

The drastic reductions observed upon selfing can be partially overcome with a milder form of inbreeding. Tysdal and Kiesselbach (1944) reported the average number of seeds per 10 flowers was 3.2 and 8.0 for selfing and sib-mating, respectively. Bolton (1948) found that crosses between second generation selfed plants originating from the same parents were intermediate in seed and forage yield between comparable inbred lines and outcross progenies.

The yields of selfed, sib-crossed, and backcrossed progenies have been investigated by Busbice and Wilsie (1966). They observed that the average yield of the backcrossed progenies was 73 percent of the S_0 performance while the yield of the S_1, S_2 and the sib-crossed progenies was 74, 46, and 62 percent, respectively. Therefore, they postulated that there may be a high frequency of loci in a natural population of alfalfa which are tetragenic and trigenic, and that the rapid loss of vigor observed upon inbreeding is due to the rapid loss of these heterozygous loci. The milder forms of inbreeding such as sib-mating and backcrossing tend to maintain the tetragenic and trigenic loci at a somewhat higher tendency than occurs following selfing.

Heterosis from outcrossing is essentially the converse of inbreeding depression. The greater the sensitivity of a species to inbreeding the greater heterotic effect is expected. Young and Murray (1966) studied heterosis and inbreeding depression in diploid and tetraploid cotton. Heterosis was found in both species. However, the tetraploid hybrids exhibited less heterosis than the diploid hybrids and were less sensitive to inbreeding. They pointed out that the tetraploid species may carry an accumulation of favorable dominant growth genes in duplicate, a factor which results in a type of built-in heterosis, and thus would not be expected to express much heterosis. Levings, _et al_. (1967) studied the effect of crossing and inbreeding in autotetraploid corn. Rank of generation means for the three characters measured were in the order, double cross > single cross > F_2 > F_3 > inbred lines. Regression analysis indicated that nearly all the variability among generation means could be accounted for by differences in level of inbreeding. This study has important implications for breeders of autotetraploid species. They suggested that if inbred lines are used to maintain genetic identity of stocks to be used in hybrid combinations, minimal levels of inbreeding should be used in order to reduce the level of inbreeding in crosses between lines. Thus, development and maintenance of lines by full-sib mating might be more desirable than by selfing.

Hybrid vigor in corn, as well as in other crop plants, has been realized. In alfalfa, Westgate (1910) found that the variegated alfalfa hybrids from the cross Medicago falcata X M. sativa performed better than both parents. Waldron (1920) also found that the F_1 hybrids between these two alfalfa species showed a much greater weight per plant than either parental plant. This increase in weight was 47.5 percent. The absolute variability of the hybrids was much greater than that of the parents. Winter injury was comparatively slight, but the plants of M. falcata showed significantly less killing than the other groups.

Tysdal, et al. (1942) and Tysdal and Kiesselbach (1944) found a marked increase in forage yield of the F_1 hybrids over that of the parental lines. They also reported that some double crosses produced by crossing two F_1 hybrids exhibited as much vigor as the single crosses from inbred lines. From 2 crosses involving erect and prostrate clones, Wilsie (1958) found a striking degree of heterosis with the F_1 hybrids, yielding 81 percent and 43 percent, respectively, above the higher yielding parent.

Recognizing the close similarity between the breeding characteristics of alfalfa and corn, Tysdal, et al.(1942) proposed a breeding system for alfalfa similar to that employed in breeding hybrid corn. By means of this system of improvement it should be possible to capitalize upon hybrid vigor, and at the same time, maintain a degree of uniformity for such characteristics as disease resistance, winter hardiness, and quality that was not obtainable by any other method of breeding.

The procedure outlined by Tysdal for producing hybrid alfalfa involves the production of four self-sterile clones which together would combine well to produce two self- and sib-sterile single crosses, which in turn would combine to produce an outstanding double cross. The four clones would be vegetatively propagated and isolated in two crossing blocks for the production of the two single crosses. Seeds from the two single crosses would be mixed and planted in a manner suitable for commercial seed production and from these fields would be obtained the double cross seed for commercial plantings.

Lesins (1961) proposed a method for the production of commercial varieties which involves inbreeding for at least three generations. Several parental clones which are tolerant to inbreeding would be selected. This parental stock may then be increased vegetatively to quantities required for production of sufficient volumes of I_1 (S_1 seed), or foundation seed. A composite of seed may be made by mixing equal proportions from each clone and maintained in this manner in consecutive releases of foundation seed. The next two generations, I_2 and I_3, would correspond to registered and certified seed lots, respectively. Additional improvement might be achieved by conducting a recurrent selection program with the parental stocks initially selected for tolerance to inbreeding.

Lantican (1961) and Williams (1964) have suggested the use of sib-mating and backcrossing as a means of obtaining inbred lines for the production of hybrids. Dudley (1964), in a theoretical study of tetraploid genetics, has shown that crosses between S_0 plants should be superior to the crosses between random inbred lines from them. Double crossing between single crosses made from heterozygous S_0 plants would seldom outperform the best single cross; however, double crosses between single crosses made from highly inbred lines would often outperform the best single cross.

Diversity of germ plasm has been found important in obtaining heterosis in many crop plants. Lonquist and Gardner (1961) studied twelve open-pollinated varieties of corn and their F_1 intercrosses, the varieties representing a range of diversity of germ plasm adapted to the Cornbelt. Average heterosis relative to the midparent was 108.5 percent and relative to the high parent 102.8 percent. Hagberg (1952), on crossing differentiated populations of rye which were very slightly inbred and with a comparatively restricted number of alleles, found a heterotic effect in grain yield in comparison with crosses between plants within the populations. The degree of heterosis was found to be parallel to the degree of genetical differentiation between the populations. Crosses between differentiated populations of red clover, however, did not show a similar heterosis effect. This was hypothetically explained by the fact that the genetical variation within those populations was probably greater, in comparison with the differentiation between populations, than was the case in the rye populations. More recently Pfahler (1966) also found heterosis in intervarietal crosses in rye.

In a diallel cross of two species of cotton, Marani (1963) found that the extent of heterosis for yield was higher in interspecific crosses than in intraspecific crosses.

The expression of heterosis in crosses between varieties of flue-cured tobacco has been reported to be minimal (Aycock, *et al*, 1963; Matzinger and Mann, 1962). However, significant expressions of hybrid vigor were noted in certain interspecific hybrids of tobacco (Mann and Weybrew, 1958).

Interspecific hybridization in alfalfa, especially the cross between *Medicago sativa* and *M. falcata*, has been made successfully (Sprague, 1956; Oldemeyer, 1956; Lesins, 1956). Sprague (1956) studied cytologically the hybrids from crosses made using three diploid alfalfa species, *M. sativa*, *M. falcata*, and *M. gaetula*. He suggested that instead of considering these as three distinct species they preferably may be considered as genetic variants of a single polymorphic species. These so-called species could be used in any combination in a breeding program without meiotic difficulties. Artificial tetraploids should have the same degree of homology and cross with cultivated alfalfa. Oldemeyer (1956) found that crosses between species in the section *Falcago* were generally successful. Hybrids of *M. sativa* with *M. falcata* (4n) were readily obtainable. It was suggested that germ plasm for the improvement of alfalfa would have to come from species in the subgenus Falcago. Especially the yellow-flowered medic, *Medicago falcata*, has been found to have the ability to withstand winter and drought (Oakley and Garver, 1917).

Lubenec (1959) studied interspecific and intraspecific hybrids of alfalfa. He found that intervarietal and interspecific hybrids outyielded the local variety. The most promising hybrids, productive, tolerant of frost and drought, and resistant to disease, were obtained by interspecific hybridization of cultivated alfalfa with wild *Medicago falcata*. They outyielded the local variety by 15 to 30 percent in the first three generations and were nearly as productive as this from the fourth generation onwards.

Dudley and Davis (1967) grouped plant introductions of alfalfa for heterosis studies. Based on origin, winterhardiness, leaf hopper yellowing score, and growth index they classified seven introductions of *Medicago sativa* var. *gaetula* as gaetula; five introductions as gaetula-like; 50 as Chilean; 20 as chilean-like; 20 as Flemish; 19 as Afghan; nine as Afghan-like; and 14 as non-hardy. They pointed out the importance of this type of classification to lie in its usefulness to plant breeders for determining the best sources of valuable combinations of genes. It may be possible, by studying crosses between and within groups, to determine the kinds of crosses most likely to produce maximum heterosis.

Emphasis has been placed on the necessity for selecting desirable individual plants, or inbred lines on the basis of one or more of the several types of evaluation that may be used. Tests frequently used include the performance of progenies from pair-crosses, top-crosses, open-pollinations, polycrosses, and diallel crosses. Pair-cross progenies refer to single cross progenies from a number of clones which are grouped together in sets of two. Johnson (1952) has reviewed results obtained using some of these progeny-testing methods in corn and forage improvement. Each method of evaluation will be reviewed briefly.

Tysdal and Crandall (1948) evaluated eight alfalfa clones and various types of progenies and found that the performance of the clones themselves gave a good indication of the performance of their progenies, particularly with respect to insect and disease resistance. Wilsie (1951) found a low but significant correlation between vegetatively propagated alfalfa clones and both their open-pollination and S_1 progenies. One factor that might have contributed to the low correlation value was a lack of satisfactory root development of the clonal plants. McAllister (1950) obtained highly significant r values of .72 and .84 between the yield of parental clones and yields of F_1 progenies and S_1 progenies, respectively.

Self progenies have been used to evaluate the breeding potential of parental plants. The number of progenies that can be evaluated may be limited using this method, especially if the parental plants are relatively self-sterile. McAllister (1950) found that the self-fertility of the parental alfalfa clones was not significantly correlated with the yield of parental clones, F_1 or S_1 progenies. Davis (1955) obtained a significant correlation coefficient of .47 between vigor of parental alfalfa clones and a three year average of their S_1 progeny performance. Wilsie and Skory (1948) obtained a correlation coefficient of .42 between yields of clones and their self progenies in alfalfa. Correlations of -.1643 for forage yield and .4076 for fall growth habit between inbreds and hybrids were obtained by Tysdal, et al.(1942) in alfalfa. Johnson (1952) emphasized that inbreeding in forage crops is not necessary for the development of superior breeding materials.

Paired crossings have not been used commonly to evaluate the potential of large numbers of parent plants. Shaepman (1952) has indicated that such a test would give only limited information on specific combining ability, whereas, general combining ability is most important.

Topcross performance tests have been used quite extensively in corn but to a limited extent in forage breeding. Bolton (1948) compared the performance of high-combining tester plants versus low-combining tester plants for use as testers in alfalfa crosses. His data indicated that two or more plants were more useful than one as testers and that plants which are poor combiners are equally as good testers as plants that are good combiners. Tysdal and Crandall (1948) found that alfalfa clones ranked on the basis of topcross performance maintained practically the same rank when evaluated on the basis of selfed progenies or polycross progenies.

Outcrossed progenies, or open-pollination progenies, have been used by forage breeders as a method of evaluating parental clones. Wilsie and Skory (1948) found a correlation coefficient of .75 between forage yields of open-pollination and self progenies from the same lines of alfalfa. In the same study, a correlation of .36 between the yields of clones and their open-pollination progenies was found. Tysdal, et al.(1942) obtained correlations in alfalfa between hybrids and progeny of open-pollinated inbreds of .3476 for forage yield and .4679 for growth habit..

Tysdal, et al (1942) suggested the term polycross to refer to the progeny from seed of a line that was subject to outcrossing with other selected lines growing in the same nursery. The method is used to test the combining ability of the selected lines. Wellensiek (1952) discussed the theoretical basis of the polycross test using a two gene model. He demonstrated that the recognition of desirable genotypes by polycrossing has a sound theoretical basis. He also emphasized the importance of maintaining vegetative propagules of selected clones since the polycrossing disturbs the original genotypes.

Tysdal and Crandall (1948) compared the performance of eight alfalfa clones in two clone synthetics, polycross seed, topcross seed, and selfed seed from the eight clones. They found that for selecting desirable material, polycross progenies gave results equally as good as selfed progenies. Clones selected for high combining ability by the polycross method produced a synthetic variety having a significantly higher forage yield than standard varieties or clones of low combining ability chosen by the same technique.

Graumann (1952) pointed out the advantages of using the polycross technique for evaluating forages which are unadapted to large-scale controlled crossing by hand. He felt that the method provided an opportunity, at reasonable cost, to produce enough seed to get a reliable measure of general combining ability of a large number of individuals. Davis (1955) found that the polycross progeny yields could be used to predict the yields of synthetics.

The importance of testing materials for combining ability prior to the production of hybrid and synthetic varieties has been recognized. Kehr and Graumann (1958) defined combining ability as the performance of a clone or line in combination with other clones or lines. It is the ability of a given selection to transmit to its progenies the traits for which it has been selected.

The use of diallel crosses to determine the value of parental strains in hybrid combination has been considered a useful tool for many years. Hayes (1926) utilized this method to determine which strains combined well to produce the greatest vigor in F_1 hybrid corn. This breeding method has been applied in forage improvement (Johnson, 1952; Kirk, 1932; Tysdal, et al. 1942).

Sprague and Tatum (1933) presented a method of estimating general combining ability and specific combining ability in the yield of single crosses of corn. General combining ability was used to designate the average performance of a line in hybrid combinations. Specific combining ability was used to designate those cases in which certain combinations did relatively better or worse than would be expected on the basis of average performance of the lines involved. They pointed out that in a population unselected for combining ability, genes with additive effects (gca) are either more common or produce greater effects than genes with dominance or epistatic effects (sca). However, in previously selected material, genes with dominance and epistatic effects are more important than genes with additive effects since remaining lines have a higher degree of similarity in performance than the original population.

General combining ability and specific combining ability for many agronomic traits in alfalfa have been estimated. Wilsie and Skory (1948) used a diallel cross to evaluate forage yields of single crosses among seven low crown alfalfa lines. They found that the strains differed materially in combining ability and a low correlation of .37 was obtained between general combining ability as determined by open-pollinated progenies and specific combining ability as determined by single cross performance.

Morley, et al.(1957) used the diallel method of crossing to evaluate spaced progenies of 10 alfalfa strains which differed in winter and summer growth rates. The strains were found to differ with respect to combining ability for growth rates in both summer and winter but differences between strains were much more evident in winter than in summer.

Pearson and Elling (1958) studied the performance of synthetic varieties of alfalfa as compared to the performance of the single crosses constituting each synthetic. They concluded that for some characters where inheritance was conditioned by additive factors, synthetic performance could be predicted on the basis of single cross performance. Specific combining ability for forage yield and winter hardiness was exhibited among the crosses.

Kehr and Graumann (1958) presented data from a diallel series of crosses among six selected alfalfa clones which showed quite high and similar general combining ability estimates for forage yield. As might be expected, all the clones exhibited specific combining ability for forage yield.

Carnahan, et al.(1959) reported on seedling vigor and fall growth habit of 91 single crosses from 14 alfalfa clones which were scored in three and four states, respectively. As a group, the clones had not been selected previously for vigor and fall growth habit, estimated general combining ability components were far larger than specific combining ability components for both characters, both components were highly significant.

A diallel series of crosses in alfalfa was analyzed by Kehr (1961) for fall growth habit, rate of recovery, spring growth habit, and forage yield. Estimated variance components for general combining ability were significant for fall growth habit and rate of recovery but not for spring growth habit nor forage yield. Estimated variance components for specific combining ability were significant for all traits measured. Results obtained for forage yield, in which estimated variance components for specific combining ability were much larger than for general combining ability, substantiated previous reports that in crosses involving materials previously tested for general combining ability for yield, specific combining ability has the larger effect in determining yield differences.

Frakes, et al.(1961) studied F_1 crosses made from 2 upright and 2 prostrate clones for general and specific combining ability. Dry matter yield and components of yield (natural height, longest stem, natural width, and stem number) were determined. The diallel analysis for general and specific combining ability showed that general combining ability effects were larger for natural height and length of longest stem, but relatively small for natural width and number of stems per plant. Dry matter yield was intermediate among the four components in respect to general combining ability effects. The study showed that two components, natural height and longest stem, lend themselves to synthetic breeding whereas the other two are better suited to a hybrid breeding program designed to take advantage of gene interaction.

Theurer and Elling (1963) reported diallel analysis of F_1 crosses among five diverse clones of alfalfa in a series of three publications. All five clones were quite resistant to bacterial wilt but differed considerably in winter hardiness, persistence, and forage yield. The ten single crosses, 26 possible Syn-2 generation synthetics, and the S_1 progenies were evaluated. All of the entries were highly resistant to bacterial wilt (Theurer and Elling, 1963a). The best single cross was not significantly more resistant than the better synthetic varieties. The general combining ability variance of the five clones was considerably larger than that for specific combining ability suggesting that rapid progress could be made in developing wilt resistant lines by combining clones having high general combining ability. For winter hardiness and persistence the best entry was a single cross (Theurer and Elling, 1963b). However, the advantage of the single cross was not great enough to be a practical advantage over synthetic varieties. As expected, the variability in forage yield was greatest for the single cross class (Theurer and Elling, 1964). In the Syn-2 generation the variability decreased respectively as the number of clones in synthetics increased.

Buker (1963) studied general and specific combining ability in alfalfa. Eight clones were selected from a population of 114 phenotypically superior plants and studied in an 8-clone diallel in both spaced plant and drilled plot tests. All of the statistical tests for general combining ability were significant and about 2/3 of those for specific combining ability were significant. It was suggested that in the population represented by these clones, breeding systems which utilize both general and specific combining ability should be most effective.

General and specific combining ability were estimated in a 20 clone diallel (Beyer, 1964). Eight clones came from Minnesota, nine from Indiana, three from North Carolina, and one from Pennsylvania. Diversity of breeding material was found to be the major factor in the relative importance of general versus specific combining ability. When all 21 clones were analyzed, specific combining ability was significant for all 20 variables measured while 14 of 20 were significant for general combining ability. When the 12 clones from Indiana, North Carolina, and Pennsylvania were analyzed as a group, 11 of 20 variables showed significant specific combining ability effects and all 20 variables showed significant general combining ability. When the eight clones from Minnesota were analyzed separately, 11 of 20 variables were significant for specific combining ability and 17 of 20 for general combining ability. A breeding program using both general and specific combining ability was suggested.

Alfalfa is a naturally cross-pollinated crop and usually low in self-fertility. Waldron (1919) found 85.4 percent natural crossing using _Medicago falcata_ and _M. sativa_ which produce yellow and purple flowers, respectively. Tysdal, _et al_ (1942) reported an average of 89.1 percent cross-pollination using yellow and white flowers as testers. Similar results have been reported by Burkhart (1937) in Argentina, Knowles (1943) and Bolton (1948) in Canada, Johansen (1963) in Denmark, and Kehr and LaBerge (1966) in the United States.

Lesins (1961) has suggested the use of male-sterile plants as testers instead of flower color. He found that cross-fertilization ranged from eight to 44 percent. Bolton (1948) observed an average self- and cross-fertility of 1.58 and 5.54 seeds per flower, respectively. Similarly Knowles (1943) working with random Grimm plants and self-fertile selections found an average of 0.56 and 1.65 seeds per flower selfed, respectively. However, when these two groups of plants were cross-pollinated, he obtained 3.70 and 4.60 seeds per flower for Grimm plants and self-fertile selections, respectively.

The relationship between cross- and self-fertility is of considerable interest but not completely understood. Wilsie (1951) reported a fairly high degree of association ($r = 0.71$) between cross- and self-fertility, while Bolton (1948) found a correlation coefficient of only 0.288. Lantican (1961) and Aycock and Wilsie (1967) obtained significant positive correlations between self-fertility and cross- and sib-fertility. Heritability estimates of cross-, sib-, and self-fertility were relatively large (Aycock and Wilsie, 1967).

Recently, Carleton and Eslick (1967) studied effects of self- and cross-compatibility on the frequency of hybrids in alfalfa. They found that self- and cross-compatibility were closely associated. In crosses between white and purple flowered clones, pods per flower and seed per flower declined rapidly as self-compatibility of the female parent decreased. Selection for low self-compatibility resulted in low seed yield regardless of mating pattern. Seed productions were also influenced by the level of male cross-compatibility of the male parent. The percentage of crossed seed in the hybrids was not closely associated with self-compatibility of the female parent. Male cross-compatibility was associated with the percentage of crossed seed in the hybrids. Carleton and Eslick suggested a type of "specific combining ability" for the production of hybrids.

Gartner and Davis (1966) studied the effects of self-compatibility on chance crossing in alfalfa. Eight of the 19 clones ranging from 6.9 to 91.2 percent pod set under self-pollination were selected. These eight clones were used as females and hand crossed with and without emasculation to two different yellow-flowered clones as males. When the emasculated progenies were compared to the unemasculated progenies, only one of the 16 comparisons was significantly different. The data suggest no relationship between percent self-compatibility and actual self seed set when hand crosses were made without emasculation.

The number of seeds obtained from a particular cross often depends on which plant is used as the male and which as the female parent. Differences in fertility of reciprocal crosses have been found by many workers. Rotar and Kehr (1963) found in Ranger alfalfa that the cross R25XR5 yielded 4.40 seeds per pod while the reciprocal (R5XR25) yielded only 0.41 seeds. Similar results have been reported by Dean (1942) and Whitehead and Davis (1954).

Reciprocal differences have also been found for certain agronomic and seedling traits. Carnahan (1963) found differences in seed weight and seedling height. These reciprocal differences were largely atributed to the relation between seed size and photosynthetic area in the seedlings. Wilcox and Wilsie (1964) found reciprocal differences for fall growth habit and yield. Maternal effects were significant for fall growth habit, suggesting cytoplasmic effects expressed in degree of erectness; however, non-maternal reciprocal effects were found for yield only, and these differences were due possibly to cytoplasm X genotype interactions.

Considerable emphasis has been placed on breeding alfalfa to improve forage and seed yield. A knowledge of interrelationships among characters that effect forage and seed yield is necessary if selection for the simultaneous improvement is to be most effective. Tysdal and Kiesselbach (1944) pointed out that high-yielding plants were taller, more upright, and more sparsely leaved, and they had thicker and more woody stems than low-yielding plants, though these characters did not show complete linkage.

Burton (1937) studying the relationship between total plant yield and various morphological characters in an F_2 population from a cross between *Medicago sativa* and *M. falcata*, obtained positive linear correlation ratios of plant yield with plant height, leaf area index, stem length, length of new shoots, and the date of second bloom. Total yield was negatively correlated with leaf shape index. Burton also reported a small but positive yield, indicating that the branched root system typical of the *M. falcata* parent could be incorporated into high yielding types. The same general types of correlations were found in a study of spaced plants of Kansas common alfalfa. In crosses between *M. falcata* and Hardigan a small but significant positive correlation between yield and root type was found, again indicating higher yield for the branching root type.

Dudley and Hanson (1961) studied the correlations between several characters in F_2 populations derived from crosses between three creeping rooted alfalfa clones and 19 hay-type clones. Highly significant, positive correlations were found between height, spring growth, and recovery, between plant width and yield, between leaf width and leaf length, and between crown width and procumbence. These correlations were significant for three sources of variation, i.e., variation associated with hay-type parents, F_1's within crosses, and plants within plots.

Frakes, et al. (1961) studied the relationships between dry matter yield per plant and other associated characters in a space-planted alfalfa nursery consisting of S_1's, F_1's, F_2's and vegetatively propagated parents of prostrate- and upright-growing type. The path-coefficient analysis of correlation coefficients showed natural plant width to be primarily direct in its effect on yield, whereas stem number was primarily indirect. A large portion of the significant association of height and long stem length with yield was indirect in its effect via width.

Nielsen and Mortensen (1963) investigated the interrelations among various characters in alfalfa and reported that in spaced plants of clones and various types of crosses, height was closely correlated with vigor. Fairly close correlations were found also between seed yield and seed set, between seed set, date of termination of flowering and date of ripening, and between hay yield at the time of seed harvest and seed yield and seed set.

Larson and Smith (1963) studied the association of various morphological characters with the winter hardiness of alfalfa. Average height, percentages of extra tall and short growing plants, and the growth habit of plants in the variety populations were highly correlated with winter hardiness. They suggested that these characters could aid the plant breeder in selecting for hardiness in an alfalfa improvement program.

Liang and Riedl (1964) used a simple correlation coefficient method and found that plant height, number of leaves, number of internodes, and number of stems were positively correlated with forage yield. Plant height, seed size, fertility, and number of stems were positively correlated with seed yield.

MATERIALS AND METHODS

Source of Materials

Source materials for this study were obtained from three alfalfa varieties, Alfa, Vernal and Kuban. The first two are varieties of *Medicago sativa* and the latter a variety of *Medicago falcata*.

Alfa was produced by Weibullsholm Plant Breeding Institute, Landskrona, Sweden (Bolton, 1962). It is derived from Flamande alfalfa grown in Denmark, and appears to be more winter hardy than that from French sources. Alfa is characterized by rapid development and a good recovery after cutting.

Vernal is a synthetic variety produced at the University of Wisconsin, Madison, U.S.A. (Bolton, 1962). It has a broad genetic base and was derived from Cossack, Ladak, Kansas Common, and *M. falcata*. The flowers are highly varigated. Vernal is considerably more winter hardy, somewhat more resistant to damage from leafhoppers, better in forage yield, more competitive in mixtures with bromegrass, and more tolerant of extra cutting and grazing, than some alfalfa varieties.

Kuban is a "yellow-flowered" variety of *Medicago falcata* introduced from U.S.S.R. as P. I. No. 258751. There is a wide range of variation of growth habit in the falcata species, ranging from prostrate to upright (Oakley and Garver, 1917). It is much wider in its adaptations than *M. sativa*. In years that are favorable for hay production, *M. falcata* may produce as heavy yields as the varieties of M. sativa, and in some cases even greater yields for the first cutting. A serious drawback to the general utilization of *M. falcata* as a cultivated forage crop is its inability to recover quickly after cutting. However, it is valuable in hybridization programs because of its cold and drought resistance characteristics.

Production of F_1 Progenies

Twenty random plants from each variety were numbered from 1 to 20. Paired crosses between varieties and within varieties were made in the greenhouse during winter and spring of 1965. There were six groups, ten cross combinations in each group:

Group I	:	Alfa X Vernal
Group II	:	Alfa X Kuban
Group III	:	Vernal X Kuban
Group IV	:	Alfa X Alfa
Group V	:	Vernal X Vernal
Group VI	:	Kuban X Kuban

The first ten plants in each variety were used for intervariety crosses and at the same time for intravariety crosses with other ten plants in the same variety. For example, A_1 X V_1, A_2 X V_2, ..., A_{10} X V_{10}, are intervariety crosses between Alfa (A) and Vernal (V), and A_1 X A_{11}, A_2 X A_{12}, ..., A_{10} X A_{20}, are intravariety crosses within the variety Alfa. Therefore, sixty paired crosses plus reciprocals were made.

In making a cross, the standard petal of each flower used as female was removed at the base. The flowers were then tripped and the pollen collected in a small paper boat. Pollen remaining on the flowers after collection was removed by a vacuum pump. Pollen was applied to the stigmas of the female plants immediately following emasculation. The number of flowers crossed per raceme and the date were recorded on small marking tags which were then attached to the appropriate raceme.

Approximately four to five weeks after crossing, fully mature pods were harvested and threshed; the total number of flowers crossed and the total number of seeds obtained were recorded for each cross combination, including reciprocals.

Because of insufficient seed in some crosses, only 53 of 60 crosses were used in the experiment. Entry numbers of these 53 crosses and three check varieties are presented in Table 1. The F_1 seeds and seeds from three check varieties, Alfa, Vernal, and Kuban, were planted in the greenhouse during the spring of 1965. The seeds were scarified and planted in peat pots arranged in wooden flats. On June 7 and 8, 1965, approximately four weeks after seeding, the seedlings were transplanted in a spaced planted field nursery. A 7 X 8 rectangular lattice design with 8-plant plots and 4 replicates was used. Some entries that had insufficient plants were substituted by check varieties and regarded as missing plots.

Field Procedures

During the summers of 1965, 1966 and 1967, certain agronomic characteristics were observed in the F_1 progenies and the data collected are presented in Table 2. The score from one to nine on each plot was used for winter injury, winter killed, disease killed, and persistence. Those plants which were alive in the fall of 1965 but missing in the spring of 1966 were considered winter killed. The plants killed by diseases late in summer of

Table 1. Entry numbers and corresponding pedigrees for the F_1 progenies and three check varieties

Entry no.	Pedigree	Entry no.	Pedigree
1	A_1 X V_1	21	V_6 X K_6
2	A_2 X V_2	22	V_7 X K_7
3	A_3 X V_3	23	V_8 X K_8
4	A_4 X V_4	24	V_9 X K_9
5	A_5 X V_5	25	A_1 X A_{11}
6	A_6 X V_6	26	A_2 X A_{12}
7	A_7 X V_7	27	A_3 X A_{13}
8	A_8 X V_8	28	A_4 X A_{14}
9	A_9 X V_9	29	A_5 X A_{15}
10	A_{10} X V_{10}	30	A_6 X A_{16}
11	A_2 X K_2	31	A_7 X A_{17}
12	A_4 X K_4	32	A_8 X A_{18}
13	A_5 X K_5	33	A_9 X A_{19}
14	A_7 X K_7	34	A_{10} X A_{20}
15	A_8 X K_8	35	V_1 X V_{11}
16	A_9 X K_9	36	V_2 X V_{12}
17	A_{10} X K_{10}	37	V_3 X V_{13}
18	V_3 X K_3	38	V_4 X V_{14}
19	V_4 X K_4	39	V_5 X V_{15}
20	V_5 X K_5	40	V_6 X V_{16}

Table 1. Continued

Entry no.	Pedigree	Entry no.	Pedigree
41	V_7 X V_{17}	49	K_5 X K_{15}
42	V_8 X V_{18}	50	K_6 X K_{16}
43	V_9 X V_{19}	51	K_7 X K_{17}
44	V_{10} X V_{20}	52	K_8 X K_{18}
45	K_1 X K_{11}	53	K_{10} X K_{20}
46	K_2 X K_{12}	54	Alfa (A)
47	K_3 X K_{13}	55	Vernal (V)
48	K_4 X K_{14}	56	Kuban (K)

1966 were recorded separately. Winter injury scores were based on the number of plants in each plot that received a vigor score of nine. The total number of plants missing in each plot was determined during the summer of 1967 and regarded as persistence. Flower color scoring was that proposed by Barnes (see Appendix).

Data for all characteristics were collected on individual plants with the exception of winter injury, winter killed, disease killed, and persistence, which were determined on a plot basis. The analyses of all agronomic characteristics were computed on plot means.

All data were analyzed as a randomized complete block design because of seven missing plots involved. These missing plots were estimated using covariance analysis. The analysis of variance and expected mean squares

Table 2. Agronomic characteristics studied in the F_1 progenies and the dates on which each characteristic was measured

Character	Unit of measure	Date measured or scored
Seedling vigor	1 - 9[a]	July 28, 1965
Spring vigor	1 - 9	May 17, 1966
Winter injury	1 - 9[b]	May, 1966
Winter killed	1 - 9[c]	May, 1966
Disease killed	1 - 9	August, 1966
Yield	Pounds per plant	June 13 and July 18, 1966 June 19 and July 24, 1967
Natural Plant height	Centimeters	October 4, 1965 and July 8, 1966
Natural plant width	Centimeters	October 5, 1965 and July 9, 1966
Rate of recovery after cutting	1 - 9[d]	August 8, 1966
Flower color	1 - 5[e]	September, 1966

[a]1 = most vigorous, 9 = least vigorous.

[b]1 = none receiving a vigor score of nine, 9 = 4 or more receiving a vigor score of nine.

[c]1 = none missing, 9 = 4 or more plants missing.

[d]1 = fast recovery, 9 = slow recovery.

[e]1 = white, 2 = purple, violet or lilac, 3 = cream, 4 = variegated, 5 = yellow.

are presented in Table 3. The sum of squares for entries in each analysis was partitioned into components appropriate for an estimation of the variation among and within each group of entries. Further partitions among groups sum of squares were made to test differences between groups.

<u>Combining ability analysis</u>

General and specific combining ability were estimated for some agronomic characteristics. Means of each group of F_1 progenies were used in the analysis of variance. The model used is as follows:

$$Y_{ijkl} = \mu + \beta_i + g_j + g_k + S_{jk} + \delta_l + \epsilon_{ijkl}$$

where

μ = population mean

β_i = block effect

g_j = general combining ability of variety j

g_k = general combining ability of variety k

S_{jk} = specific combining ability of varieties j and k

δ_l = difference between crosses within and crosses between varieties

ϵ_{ijkl} = experimental error

Based on the assumption that $\Sigma\,\mathrm{gca} = 0$, thus $\mathrm{gca}_{(\mathrm{Kuban})} = -\mathrm{gca}_{(\mathrm{Alfa})} - \mathrm{gca}_{(\mathrm{Vernal})}$, the gca's were estimated. The residual effect obtained by subtracting gca sum of squares from among groups sum of squares was considered to include sca sum of squares and heterosis sum of squares. Heterosis sum of squares were calculated by comparing crosses between and crosses within varieties. The analysis of variance and expected mean squares are

Table 3. Analysis of variance and expected mean squares for F_1 progenies

Source of variation	D.F.	Expected mean square
Replications	3	$\sigma^2 + t\ \sigma_R^2$
Entries	55	$\sigma^2 + r\ \sigma_T^2$
Within group I	9	$\sigma^2 + r\ \sigma_I^2$
Within group II	6	$\sigma^2 + r\ \sigma_{II}^2$
Within group III	6	$\sigma^2 + r\ \sigma_{III}^2$
Within group IV	9	$\sigma^2 + r\ \sigma_{IV}^2$
Within group V	9	$\sigma^2 + r\ \sigma_V^2$
Within group VI	8	$\sigma^2 + r\ \sigma_{VI}^2$
I,II,III vs IV,V,VI	1	$\sigma^2 + r\ \sigma_A^2$
I vs II, III	1	$\sigma^2 + r\ \sigma_B^2$
II vs III	1	$\sigma^2 + r\ \sigma_C^2$
IV, V vs VI	1	$\sigma^2 + r\ \sigma_D^2$
IV vs V	1	$\sigma^2 + r\ \sigma_E^2$
A,V,K vs IV,V,VI	1	$\sigma^2 + r\ \sigma_F^2$
A, V vs K	1	$\sigma^2 + r\ \sigma_G^2$
A vs V	1	$\sigma^2 + r\ \sigma_H^2$
Error	158[a]	σ^2
Total	223	

[a]Corrected degree of freedom because of missing plots.

presented in Table 4.

Table 4. Combining ability analysis of variance and expected mean squares

Source of variation	D.F.	Expected mean square
Replications	3	
Among groups	5	
gca	2	$\sigma^2 + 5r \frac{g^2{}_i}{2}$
sca	2	$\sigma^2 + r \frac{s^2{}_{ij}}{2}$
Heterosis	1	$\sigma^2 + 3r \Sigma \delta^2{}_1$
Error	15	

Production of F_2

In Fall, 1965, cuttings were made of each F_1 progeny. These 53 F_1 clones were selfed in the greenhouse during Winter and Spring of 1966. Selfing of flowers was accomplished by applying pressure on the keel with the tip of a toothpick, and drawing the tip across the exposed stigma. Approximately 200 flowers per clone were tripped.

Fully mature pods were harvested and threshed. The seeds were germinated in the greenhouse in Spring, 1966. Because of self-sterility in some entries and difficulty in germination in others, only 33 F_2 populations were studied. The entry numbers and corresponding pedigrees of F_2 progenies and three check varieties are presented in Table 5. The cross Kuban X Kuban

Table 5. Entry numbers and corresponding pedigrees of F_2 progenies and 3 check varieties

Entry	Pedigree	Entry	Pedigree
1	A_1 X V_1	19	A_2 X A_{12}
2	A_2 X V_2	20	A_3 X A_{13}
3	A_4 X V_4	21	A_4 X A_{14}
4	A_5 X V_5	22	A_5 X A_{15}
5	A_6 X V_6	23	A_6 X A_{16}
6	A_8 X V_8	24	A_8 X A_{18}
7	A_{10} X V_{10}	25	V_1 X V_{11}
8	A_2 X K_2	26	V_2 X V_{12}
9	A_7 X K_7	27	V_3 X V_{13}
10	A_8 X K_8	28	V_4 X V_{14}
11	A_9 X K_9	29	V_5 X V_{15}
12	V_3 X K_3	30	V_6 X V_{16}
13	V_5 X K_5	31	V_8 X V_{18}
14	V_5 X K_5	32	V_9 X V_{19}
15	V_6 X K_6	33	V_{10} X V_{20}
16	V_7 X K_7	34	Alfa (A)
17	V_8 X K_2	35	Vernal (V)
18	A_1 X A_{11}	36	Kuban (K)

Table 6. Agronomic characteristics studied in the F_2 populations, and the dates on which each characteristic was measured

Character	Unit of measure	Date measured or scored
Seedling vigor	1 - 9[a]	August 3, 1966
Spring vigor	1 - 9	May 24, 1967
Yield	pounds per plant	June 21 and July 31, 1967
Rate of recovery	1 - 9[b]	July 12, 1967

[a] 1 = most vigorous; 9 = least vigorous.

[b] 1 = fast recovery; 9 = slow recovery.

(Group VI) was discarded because of its self-sterility. Thus, there were only five groups of crosses in this study.

On June 6, 1966, F_2 plants were established in the field in a spaced planted nursery. A randomized complete block design with 5-plant plots and five replications was used. The various agronomic characteristics studied and the dates on which data were collected are presented in Table 6. The analysis of variance and expected mean squares are presented in Table 7.

Fertility Studies

Self-fertility in F_1 progenies

Five F_1 families in each group of crosses were selected on the basis of availability of their parental plants. Only variegated-flowered plants were selected from the crosses between *M. sativa* and *M. falcata* in order to

Table 7. Analysis of variance and expected mean squares for F_2 progenies

Source of variation	D.F.		Expected mean square
Replications	4		$\sigma^2 + t\ \sigma_R^2$
Entries	35		$\sigma^2 + r\ \sigma_T^2$
Within group I		6	$\sigma^2 + r\ \sigma_I^2$
Within group II		3	$\sigma^2 + r\ \sigma_{II}^2$
Within group III		5	$\sigma^2 \div r\ \sigma_{III}^2$
Within group IV		6	$\sigma^2 + r\ \sigma_{IV}^2$
Within group V		8	$\sigma^2 + r\ \sigma_V^2$
Within checks		2	$\sigma^2 + r\ \sigma_{CH}^2$
Checks vs rest		1	$\sigma^2 + r\ \sigma_A^2$
I,II,III vs IV,V		1	$\sigma^2 + r\ \sigma_B^2$
I vs II, III		1	$\sigma^2 + r\ \sigma_C^2$
II vs III		1	$\sigma^2 + r\ \sigma_D^2$
IV vs V		1	$\sigma^2 + r\ \sigma_E^2$
Error	140		σ^2
Total	179		

be sure they were F_1 hybrids. Cuttings were made from these selected F_1 plants and from their corresponding parental plants. The entry numbers of these F_1 families and their parental plants are presented in Table 8.

Three propagules of each clone were established in the greenhouse. A randomized complete block design with three replications was used. During winter and spring of 1967, selfing was accomplished as described previously for the production of F_2 and the number of flowers selfed per raceme was recorded.

Approximately four to five weeks after selfing, fully mature pods were harvested and threshed. The total number of seeds set per plant was determined by counting only those that were well-filled. A self-fertility index was determined by dividing the total number of seeds by the total number of flowers selfed. The analysis of variance and expected mean squares are presented in Table 9.

Cross-fertility

A cross-fertility index was determined in a similar manner as for self-fertility. Reciprocals of each cross combination were bulked and only those cross combinations used in self-fertility study were determined for cross-fertility. Since there was no replication in this study, the data could not be analyzed statistically. However, if each cross combination in each group is considered as an observation, these data can be analyzed as a completely randomized design with five replications. The analysis of variance and expected mean squares are presented in Table 10.

Table 8. Entry numbers of F_1 families and their parental plants.

Entry no.	Pedigree	Entry no.	Pedigree
1	A_4 X V_4	31	A_4
2	A_5 X V_5	32	A_5
3	A_7 X V_7	33	A_7
4	A_8 X V_8	34	A_8
5	A_9 X V_9	35	A_9
6	A_4 X K_4	36	A_{14}
7	A_5 X K_5	37	A_{15}
8	A_7 X K_7	38	A_{17}
9	A_8 X K_8	39	A_{18}
10	A_9 X K_9	40	A_{19}
11	V_4 X K_4	41	V_4
12	V_5 X K_5	42	V_5
13	V_7 X K_7	43	V_7
14	V_8 X K_8	44	V_8
15	V_9 X K_9	45	V_9
16	A_4 X A_{14}	46	V_{14}
17	A_5 X A_{15}	47	V_{15}
18	A_7 X A_{17}	48	V_{17}
19	A_8 X A_{18}	49	V_{18}
20	A_9 X A_{19}	50	V_{19}
21	V_4 X V_{14}	51	K_4
22	V_5 X V_{15}	52	K_5

Table 8. (Continued)

Entry no.	Pedigree	Entry no.	Pedigree
23	V_7 X V_{17}	53	K_7
24	V_8 X V_{18}	54	K_8
25	V_9 X V_{19}	55	K_{10}
26	K_4 X K_{14}	56	K_{14}
27	K_5 X K_{15}	57	K_{15}
28	K_7 X K_{17}	58	K_{17}
29	K_8 X K_{18}	59	K_{18}
30	K_{10} X K_{20}	60	K_{20}

Table 9. Analysis of variance and expected mean squares for self-fertility

Source of variation	D.F.	Expected mean square
Replications	2	$\sigma^2 + t\ \sigma_R^2$
Entries	59	$\sigma^2 + r\ \sigma_T^2$
Within group I	4	$\sigma^2 + r\ \sigma_I^2$
Within group II	4	$\sigma^2 + r\ \sigma_{II}^2$
Within group III	4	$\sigma^2 + r\ \sigma_{III}^2$
Within group IV	4	$\sigma^2 + r\ \sigma_{IV}^2$
Within group V	4	$\sigma^2 + r\ \sigma_V^2$
Within group VI	4	$\sigma^2 + r\ \sigma_{VI}^2$
Within Alfa	9	$\sigma^2 + r\ \sigma_{VII}^2$
Within Vernal	9	$\sigma^2 + r\ \sigma_{VIII}^2$
Within Kuban	9	$\sigma^2 + r\ \sigma_{IX}^2$
Among groups	8	$\sigma^2 + r\ \sigma_X^2$
Crosses vs checks	1	$\sigma^2 + r\ \sigma_A^2$
I,II,III vs checks	1	$\sigma^2 + r\ \sigma_B^2$
IV,V,VI vs checks	1	$\sigma^2 + r\ \sigma_C^2$
I,II,III vs IV,V,VI	1	$\sigma^2 + r\ \sigma_D^2$
I vs II,III	1	$\sigma^2 + r\ \sigma_E^2$
II vs III	1	$\sigma^2 + r\ \sigma_F^2$
IV,V vs VI	1	$\sigma^2 + r\ \sigma_G^2$
IV vs V	1	$\sigma^2 + r\ \sigma_H^2$
Error	118	
Total	179	

Table 10. Analysis of variance and expected mean squares for cross fertility

Source of variation	D.F.	Expected mean square
Entries	5	$\sigma^2 + r\ \sigma_T^2$
I,II,III vs IV,V,VI	1	$\sigma^2 + r\ \sigma_A^2$
I vs II, III	1	$\sigma^2 + r\ \sigma_B^2$
II vs III	1	$\sigma^2 + r\ \sigma_C^2$
IV,V vs VI	1	$\sigma^2 + r\ \sigma_D^2$
IV vs V	1	$\sigma^2 + r\ \sigma_E^2$
Error	24	σ^2
Total	29	

RESULTS

F_1 Progenies

The mean values for the agronomic characteristics of each F_1 group are presented in Table 11. Individual progeny means are shown in Table 19 in the Appendix. In the first cutting of the first year, only the crosses Alfa X Kuban and Vernal X Kuban outyielded the parental check varieties. The increase in forage yield over the yield of check varieties was 32 to 40 percent for the crosses Alfa X Kuban and Vernal X Kuban, respectively. In the second cutting, however, these two groups of crosses yielded less than the crosses Alfa X Vernal. All groups of crosses except the crosses Kuban X Kuban outyielded the check varieties.

The magnitude of forage yield in the second year was similar to that in the first year. In the first cutting, the yield of crosses between varieties (A X K, A X V and V X K) was greater than that of crosses within varieties (A X A, V X V and K X K) as well as the check varieties. The increase in yield over the check varieties was 36, 89 and 90 percent for the crosses Alfa X Vernal, Alfa X Kuban and Vernal X Kuban, respectively. There was not much difference between the forage yield of the crosses between varieties and the crosses within varieties in the second cutting except that for the crosses Kuban X Kuban which had much less yield than the others.

All vigor ratings indicate that crosses between varieties (A X V, A X K and V X K) were more vigorous than crosses within varieties (A X A, V X V and K X K). The rates of recovery after cutting for the crosses Alfa X Alfa, Alfa X Vernal and Vernal X Vernal were the best. The crosses between

Table 11. Mean values for agronomic characteristics of each F_1 group

Group	Cross	Yield 1966 1st cutting	Yield 1966 2nd cutting	Yield 1967 1st cutting	Yield 1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Recovery 1966
I	A X V	0.86	0.52	1.04	0.73	2.7	3.6	3.7	2.3
II	A X K	1.18	0.43	1.44	0.70	2.8	3.2	2.9	3.1
III	V X K	1.25	0.48	1.45	0.73	3.7	3.6	3.1	2.9
IV	A X A	0.68	0.44	0.77	0.60	2.4	4.4	4.7	2.4
V	V X V	0.83	0.46	0.99	0.74	3.1	3.8	3.6	2.2
VI	K X K	0.99	0.11	0.58	0.15	6.3	4.6	6.6	8.2
	Alfa	0.55	0.37	0.68	0.54	2.4	5.1	5.4	3.0
	Vernal	0.88	0.42	1.01	0.68	3.6	4.1	4.4	3.5
	Kuban	1.23	0.10	0.59	0.13	5.2	4.3	6.7	8.3
Average checks		0.89	0.29	0.76	0.45	3.7	4.5	4.9	4.9
L.S.D. (.05)		0.24	0.10	0.30	0.16	1.5	1.2	1.2	5.1

Table 11. (Continued)

Group	Plant height 1965	1966	Plant width 1965	1966	Flower color	Winter killed	Winter injury	Disease killed	Persistence
I	40.5	52.1	47.0	41.9	2.6	1.6	1.1	1.1	1.9
II	36.8	40.5	47.8	42.2	4.0	1.5	1.1	1.1	1.8
III	31.5	42.4	52.8	42.2	4.0	1.4	1.5	1.2	2.4
IV	43.9	53.9	40.3	36.5	2.3	1.8	1.3	1.2	2.6
V	36.9	50.6	46.7	42.1	2.7	1.0	1.0	1.0	1.1
VI	22.2	22.2	55.9	27.7	5.2	1.5	1.3	1.9	4.2
	41.7	51.4	41.5	34.5	2.2	1.0	1.0	1.0	1.1
	44.7	44.7	43.6	40.2	3.0	1.5	1.5	1.0	2.5
	22.5	19.8	68.4	28.1	5.2	2.0	1.0	1.5	6.0
	32.3	38.6	51.2	34.3	3.5	1.5	1.2	1.2	3.2
	5.1	4.6	7.6	4.9	0.5	1.4	0.8	0.9	2.1

Table 12. Analysis of variance mean squares for agronomic characteristics in F_1 progenies

Source of variation	D.F.	Forage Yield 1966 1st cutting	Forage Yield 1966 2nd cutting	Forage Yield 1967 1st cutting	Forage Yield 1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Recovery 1966
Replications	3	0.1299**	0.0796**	0.1008	0.0491**	11.7929**	0.5699	10.1805**	5.852
Entries	55	0.3144**	0.1102**	0.6062**	0.2563**	9.5880**	3.8171**	9.7598**	21.564
Within group I	9	0.1809**	0.0289**	0.2903**	0.0749**	1.8884	1.8311**	4.1640**	1.468
Within group II	6	0.0589	0.0217**	0.1981**	0.1632**	0.4381	3.0857**	4.1028**	4.742
Within group III	6	0.8513**	0.1040**	1.0188**	0.1301**	6.1864**	12.9847**	10.7390**	6.531
Within group IV	9	0.0908**	0.0296**	0.0515	0.0338**	0.7396	2.5440**	1.0227	1.733
Within group V	9	0.2618**	0.0224**	0.0523	0.0347**	1.9022	1.3422	0.9671	1.477
Within group VI	8	0.1249**	0.0459**	0.2683**	0.0917**	7.9500**	3.6400**	7.8400**	7.157
I,II,III vs. IV,V,VI	1	2.2028**	0.8317**	13.1124**	2.3688**	32.4688**	30.6209**	128.1484**	99.643

Table 12. (Continued)

Source of variation	D.F.	Forage Yield 1966 1st cutting	Forage Yield 1966 2nd cutting	Forage Yield 1967 1st cutting	Forage Yield 1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Recovery 1966
I vs. II,III	1	2.9881**	0.0896**	4.1778**	0.0073	5.7668*	0.8048	10.3852**	13.988
II vs. III	1	0.0714	0.0370**	0.0350	0.0165	11.3400**	2.9257	0.2857	0.182
IV,V vs. VI	1	0.9739**	2.8964**	2.2919**	6.6976**	321.1696**	8.8389**	148.0155**	815.791**
IV vs. V	1	1.2802**	0.0231*	1.0306**	0.3754**	8.7120**	5.8320**	20.4020**	1.568
A,V,K vs. IV, V,VI	1	0.0083	0.0309*	0.0747	0.0383	0.6518	0.6518	4.1432*	8.1250**
A,V vs. K	1	0.7072**	0.2321**	0.1734	0.6144**	12.9066**	0.2400	8.6400**	68.006 **
A vs. V	1	0.2178**	0.0050	0.2178*	0.1982**	2.8800	2.0000	2.0000	0.500
Error	158	0.0289	0.0053	0.0472	0.0119	1.1676	0.8098	0.7289	0.705
C.V. (%)		17.89	18.72	21.70	18.47	18.86	22.82	19.76	22.70

Table 12. (Continued)

Source of variation	D.F.	Plant height 1965	Plant height 1966	Plant width 1965	Plant width 1966	Flower color	Winter killed	Winter injury	Disease killed	Persis-tence
Replications	3	180.1101**	69.6008**	1158.7629**	69.3361**	1.2266**	3.3531*	0.8198	0.5401	10.884**
Entries	55	251.3156**	586.7827**	283.0684**	224.5753**	5.0437**	1.2661	0.5660	1.0602**	10.882**
Within group I	9	55.2338**	19.4618	156.1670**	95.8220**	0.7204**	1.5111	0.1000	0.4000	2.455
Within group II	6	12.1124	133.3200**	42.6057	42.6057	15.6914	0.4895**	0.6057	0.1429	0.952
Within group III	6	31.2247	116.0857**	542.9466**	261.4450**	1.7295**	0.9829	2.3962**	0.6762	3.832
Within group IV	9	46.7537**	51.1684**	158.8644**	96.5248**	0.1511	2.7111**	0.0000	0.0000	0.100
Within group V	9	45.9573**	27.1293**	153.6182**	90.2226**	1.1271**	0.0000	0.0000	0.0000	0.100
Within group VI	8	94.0000**	246.7744**	104.6178**	154.4500**	0.6400**	1.0544	1.111**	4.000**	3.207
I,II,III vs. IV,V,VI	1	208.3356**	473.1620**	41.334	1839.9272**	0.3660	0.8779	0.2033	2.0561	15.478**
I vs. II,III	1	943.4000**	2638.0116**	104.1638	1.9076	47.7193**	0.1190	1.1440	0.0107	1.296

Table 12. (Continued)

Source of variation	D.F.	Plant height 1965	Plant height 1966	Plant width 1965	Plant width 1966	Flower color	Winter killed	Winter injury	Disease killed	Persis-tence
II vs. III	1	397.5112**	51.3028*	769.6028**	0.0457	0.0457	0.1029	2.2400*	1.4000	5.040
IV,V vs. VI	1	8347.8600**	2231.3900**	3855.8972**	3725.6896**	177.8783**	0.1962	2.1525*	4.2776**	137.752**
IV vs. V	1	985.6080**	209.9520**	824.3280**	935.7120**	2.8880**	12.8000**	1.8000*	0.4500	45.000**
A,V,K vs. IV, V,VI	1	68.6576*	196.6952**	160.6952**	160.2816	30.5024	0.2317	0.0507	0.3245	4.393
A,V vs. K	1	572.3264**	2128.1664**	1781.9264**	228.1664**	18.0266**	1.5000	0.1667	0.6670	48.161**
A vs. V	1	165.6200**	89.7800**	8.8200	64.9800*	1.2800**	0.5000	0.5000	0.0000	231.117**
Error	158	13.3519	11.2075	30.0083	12.5352	0.1414	1.0144	0.3551	0.4454	2.307
C.V. (%)		10.47	7.79	11.20	9.29	10.57	67.33	49.16	55.00	60.40

Medicago sativa and *M. falcata* (A X K and V X K) had a slower rate of recovery after cutting; however, they were much better than the crosses Kuban X Kuban.

For natural plant height measurements, the crosses Kuban X Kuban were shorter than the plants from other crosses. The crosses Alfa X Kuban and Vernal X Kuban were shorter than the crosses Alfa X Alfa, Alfa X Vernal and Vernal X Vernal. However, the reverse situations were found for natural plant width. The crosses Alfa X Kuban and Vernal X Kuban had greater natural plant width than the crosses Alfa X Alfa, Alfa X Vernal and Vernal X Vernal. The crosses Kuban X Kuban had the greatest natural plant width in the first year but smallest in the second year.

Greatest persistence was found in the crosses Vernal X Vernal and least in the crosses Kuban X Kuban. The crosses Alfa X Vernal and Alfa X Kuban had greater persistence than the crosses Vernal X Kuban and Alfa X Alfa. The same magnitude was found for winter killed, winter injured and disease killed.

The variance mean squares for the agronomic characteristics studied in the F_1 population are presented in Table 12. Significant variation at the one percent level for entries was observed for all characteristics studied except that for winter killed and winter injured. Upon partitioning the sum of squares for entries, significant variation was found both within groups and among groups of crosses.

For forage yield, the greatest variation was found with group III (Vernal X Kuban). Considerable amount of variation was found also within group I (Alfa X Vernal) and group VI (Kuban X Kuban). In the first year the variation within each group, except that within group II (Alfa X Kuban) in the first cutting, was highly significant. In the second year, however, few groups with significant variation were found. In the first cutting the variation within group I (Alfa X Vernal), group II (Alfa X Kuban), group III (Vernal X Kuban), and group VI (Kuban X Kuban) was highly significant. In the second cutting all groups showed highly significant variation, the greatest variation being within group II (Alfa X Kuban) and group III (Vernal X Kuban).

In comparisons among groups, the forage yield of crosses between varieties (A X V, A X K and V X K) was greater (.01 level) than that of crosses within varieties (A X A, V X V and K X K). Among crosses between varieties, the crosses Alfa X Kuban and Vernal X Kuban outyielded the crosses Alfa X Vernal, and the difference was highly significant in all cases except that of the last cutting. Significant difference in forage yield between group II (Alfa X Kuban) and group III (Vernal X Kuban) was found only in the second cutting of the first year.

Among crosses within varieties (A X A, V X V and K X K), the forage yield of the crosses Alfa X Alfa and Vernal X Vernal was greater (.01 level) than that of the crosses Kuban X Kuban. The crosses Vernal X Vernal outyielded the crosses Alfa X Alfa. In comparison with the check varieties, the forage yield of crosses within varieties was not superior to the yield of the check varieties. Significant differences were observed only in the second cutting of the first year. Among the check varieties, significant difference was found mainly between the yield of Medicago sativa (Alfa and

Vernal) and the yield of _M. falcata_ (Kuban).

The magnitude of variation in other characteristics studied (vigor, recovery after cutting, plant height and plant width) was similar to that for forage yield (Table 12). Significant variation (.01 level) was found only within group III (Vernal X Kuban) and group VI (Kuban X Kuban) for seedling vigor, but for spring vigor ratings significant variation within group I (Alfa X Vernal), group II (Alfa X Kuban) and group IV (Alfa X Alfa) also was observed. The greatest variation within groups of crosses for all vigor ratings was that of group III (Vernal X Kuban). No significant variation within group V (Vernal X Vernal) was found in any vigor rating. For rate of recovery after cutting, all groups of crosses showed significant variation within groups, and the greatest variation being within group III (Vernal X Kuban). In comparisons among groups, all vigor ratings and recovery after cutting showed highly significant differences when the crosses between varieties (A X K, A X V and V X K) and crosses within varieties (A X A, V X V and K X K), intraspecific crosses (Alfa X Vernal) and interspecific crosses (Alfa X Kuban and Vernal X Kuban), and crosses within _M. sativa_ (Alfa X Alfa and Vernal X Vernal) and the crosses within _M. falcata_ (Kuban X Kuban), were compared. The greatest difference among groups for these characteristics was that between crosses between varieties and crosses within varieties (Table 12).

For natural plant height and natural plant width the variation within each group of crosses within varieties (A X A, V X V and K X K) was much greater than that within crosses between varieties (A X V, A X K and V X K). The variation within the crosses Alfa X Alfa, Vernal X Vernal and Kuban X

Kuban was highly significant for all measurements whereas few showed significant variation within each group of crosses between varieties. In comparisons among groups, the greatest difference was found between the crosses within *M. sativa* (Alfa X Alfa and Vernal X Vernal) and the crosses within *M. falcata* (Kuban X Kuban). The difference between crosses within varieties (A X A, V X V and K X K) and crosses between varieties (A X V, A X K and V X K) also was significant for all cases except that for plant width measured in 1965.

In comparisons among groups for persistence, highly significant differences were found between crosses within varieties (A X A, V X V and K X K) and crosses between varieties (A X V, A X K and V X K), and between crosses within *M. sativa* (A X A and V X V) and crosses within *M. falcata* (Kuban X Kuban). Among check varieties, Alfa was less persistent than Vernal and Kuban was less persistent than either Alfa or Vernal. No significant variation was found within any group of crosses for persistence. However, group III (Vernal X Kuban) showed significant variation for winter injured, group IV (Alfa X Alfa) for winter killed and group VI (Kuban X Kuban) for both winter injured and disease killed.

Combining ability analysis

The general and specific combining ability mean squares for some agronomic characteristics are presented in Table 13. Highly significant variation was found among groups in all characteristics studied. Upon partitioning the sum of squares among groups into general combining ability, specific combining ability and heterosis components, in most instances

Table 13. General and specific combining ability mean squares for some agronomic characteristics in F_1 progenies

Source of variation	D.F.	Yield 1 1966	Yield 2 1966	Yield 1 1967	Vigor Seedling	Vigor Spring 1966	Vigor Spring 1967	Recovery after cutting	Plant height 1965	Plant height 1966	Plant width 1965	Plant width 1966
Replications	3	0.0173	0.0094**	0.0112**	1.2637*	0.0878	1.0637**	0.7071**	18.1116	7.7366**	136.2777**	7.9132*
Among groups	5	0.1913**	0.0879**	0.4932**	8.3994**	1.1097**	7.3527**	20.3704**	234.9975**	55.1606**	124.6356**	145.5935**
gca	2	0.2178**	0.1538**	0.0583**	16.6922**	0.3132	5.4915**	39.7886**	568.8462**	35.3705**	277.1722**	194.3060**
sca	2	0.0471**	0.0074**	0.3349**	2.0530**	0.5410*	3.8170**	4.3872**	10.4342	29.5681**	27.0476**	36.3444**
Heterosis	1	0.4266**	0.1176**	1.6854**	4.5066**	3.8400**	18.0266**	13.500**	22.4266**	45.9266**	14.7266**	66.6666**
Error	15	0.0065	0.0011	0.0051	0.3981	0.1454	0.0754	0.1471	3.8137	0.7496	2.1030	1.5863

general and specific combining ability mean squares were highly significant. For forage yields, general combining ability mean squares in both cuttings of the first year were greater than that of specific combining ability mean squares. In the second year, the reverse situation was found. For other characteristics (vigor, rate of recovery after cutting, natural plant height and natural plant width) general combining ability mean squares in all cases, except that of spring vigor rated in 1966, were larger than specific combining ability mean squares. Highly significant heterosis was observed in all instances.

F_2 Progenies

The means of each group for the agronomic characteristics studied are presented in Table 14. Individual F_2 progeny means are shown in Table 20 in the Appendix. The crosses between varieties Alfa and Kuban (group II) gave the highest forage yield in both cuttings. It was the only group that out-yielded the check varieties in the first cutting. Group I (Alfa X Vernal) and group III (Vernal X Kuban) had lower yields than the check varieties in the first cutting but higher in the second cutting. In both cuttings the yield of the crosses between varieties (groups I, II and III) was superior to the yield of the crosses within varieties (groups IV and V). For vigor ratings, the crosses Alfa X Kuban were the most vigorous and equally as good in rate of recovery after cutting as that of the crosses Alfa X Vernal.

The mean squares for the agronomic characteristics studied are presented in Table 15. Significant variation (at 1 percent level) for entries was observed for all characteristics. Upon partitioning the sum of squares

Table 14. Mean values for agronomic characteristics of each F_2 group

Group	Cross	Yield 1st cutting	Yield 2nd cutting	Seedling vigor	Spring vigor	Recovery
I	A X V	0.96	0.42	2.4	2.7	2.5
II	A X K	1.44	0.44	2.1	1.5	2.5
III	V X K	1.00	0.33	3.2	3.2	3.4
IV	A X A	0.59	0.27	3.5	4.5	3.6
V	V X V	0.74	0.28	3.3	3.8	3.4
	Checks	1.26	0.35	3.2	2.6	4.4

for entries, variation was found both within and among groups. The greatest variation within groups was observed in the crosses Vernal X Kuban (group III). Variation within group I (Alfa X Vernal) was approximately the same as that within group II (Alfa X Kuban). Much less variation was found in the crosses within varieties (Alfa X Alfa and Vernal X Vernal). The only significant variation observed was that for forage yield of second cutting and rate of recovery after cutting.

In orthogonal comparisons, crosses between varieties (A X V, A X K and V X K) differed (.01 level) from crosses within varieties (A X A, V X V and K X K) for all characteristics studied. Group I (Alfa X Vernal) was different from group II (Alfa X Kuban) and group III (Vernal X Kuban) in yield and rate of recovery after cutting. Group II (Alfa X Kuban) was different (.01 level) from group III (Vernal X Kuban) for all characteristics except for yield in the second cutting. The only significant difference

Table 15. Analysis of variance mean squares of the F_2 progenies for agronomic characteristics studied

Source of variation	D.F.	Yield 1st cutting	Yield 2nd cutting	Seedling vigor	Spring vigor	Recovery
Replications	4	0.1546**	0.0415**	4.6573**	4.9932**	12.6147**
Entries	35	0.7242**	0.0473**	3.3020**	7.7069**	9.4958**
Within group I	6	0.3619**	0.0486**	1.8945	2.4269**	4.7846**
Within group II	3	0.4240**	0.0231**	4.1978**	0.2240	2.8085*
Within group III	5	1.2360**	0.0386**	3.8485**	16.0741**	9.2756**
Within group IV	6	0.0451	0.0103*	1.9200	1.7496	5.1800**
Within group V	8	0.0425	0.0203**	1.4470	2.0289*	2.3300*
Within checks	2	1.1916**	0.1565**	1.1540	3.5047**	70.3806**
Checks vs. rest	1	1.8836**	0.0018	3.0456	7.0800**	19.0081**
I,II,III vs. IV,V	1	7.4512**	0.4471**	26.3709**	90.0450**	20.6805**
I vs. II, III	1	1.6190**	0.0880**	3.2344	3.3504	17.2536**
II vs. III	1	2.3267**	0.0127	13.2296**	30.0765**	10.8680**
IV vs. V	1	0.4018**	0.0030	1.1340	10.0000**	0.7001
Error	140	0.0281	0.0048	1.3923	0.9060	1.3478
C.V. (%)		18.27	20.44	39.46	29.23	35.58

Table 16. Means of cross- and self-fertility indices of all F_1 groups and self-fertility indices of their corresponding parents

Group	Pedigree	Self-fertility index	Cross-fertility index
I	A X V	1.45	3.81
II	A X K	0.76	1.67
III	V X K	0.99	1.77
IV	A X A	0.92	2.94
V	V X V	1.44	4.44
VI	K x K	0.40	1.33
VII	Alfa	0.49	-
VIII	Vernal	0.95	-
IX	Kuban	0.05	-

observed between group IV (Alfa X Alfa) and group V (Vernal X Vernal) was that for yield in the first cutting and for spring vigor.

Fertility Studies

The means of cross- and self-fertility indices of all F_1 groups and the means for self-fertility indices of their corresponding parents are presented in Table 16. Individual entry means for cross- and self-fertility indices are shown in Table 21 in the Appendix. The highest cross-fertility index (4.44) was found in the crosses within the variety Vernal (V X V). The crosses between Alfa and Vernal had the second highest cross-fertility index. The crosses between species, Alfa X Kuban and Vernal X Kuban, had about the same level of cross fertility. The lowest cross-fertility was found in the crosses within the variety Kuban (K X K). Overall, however, the cross-fertility of the crosses within varieties was higher than that of the crosses between varieties.

Self-fertility of F_1 progenies was greater than that of the parental plants. The highest self-fertility index was found in the crosses Alfa X Vernal and Vernal X Vernal. In any group of F_1 progenies, the mean self-fertility index was higher than that of both parents involved. For example, the self-fertility index of the crosses Alfa X Vernal was 1.45 while that of the varieties Alfa and Vernal was 0.49 and 0.95, respectively.

The variance mean squares for self-fertility are presented in Table 17. Highly significant differences were observed among entries. Upon partitioning the sum of squares for entries, significant variation (.01 level) was found within group I (Alfa X Vernal), group III (Vernal X Kuban), group V (Vernal X Vernal), group VI (Kuban X Kuban), and within parental plants, Alfa and Vernal. In non-orthogonal comparison among groups, difference in self-fertility between crosses and check varieties (parental plants) was highly successful. Both the crosses between varieties (A X V, A X K and V X K) and crosses within varieties (A X A, V X V and K X K) differed from the check varieties in self-fertility. However, only slight differences in self-fertility (.05 level) were found, comparing crosses between varieties and crosses within varieties. Self-fertility of group I (Alfa X Vernal) was significantly higher than that of group II (Alfa X Kuban) and group III (Vernal X Kuban). No significant difference in self-fertility was observed between group II (Alfa X Kuban) and group III (Vernal X Kuban). Among

Table 17. Analysis of variance mean squares for self-fertility in F_1 progenies

Source of variation	D.F.	Mean squares
Replications	2	0.1132
Entries	59	1.6358**
Within group I	4	2.0283**
Within group II	4	0.3978*
Within group III	4	2.4873**
Within group IV	4	0.2459
Within group V	4	2.4376**
Within group VI	4	1.4707**
Within Alfa	9	0.5256**
Within Vernal	9	2.2065**
Within Kuban	9	0.0639
Among groups	8	4.3848**
Crosses vs. checks	1	18.2811**
I,II,III vs. checks	1	9.5579**
IV,V,VI vs. checks	1	5.2802**
I,II,III vs. IV,V,VI	1	0.4723*
I vs. II,III	1	3.2909**
II vs. III	1	0.3831
IV,V vs. VI	1	6.1152**
IV vs. V	1	2.0488**
Error	77[a]	0.1154

[a]Corrected error degrees of freedom due to the observations with zero values.

crosses within varieties, the highest self-fertility was found in group V (Vernal X Vernal).

Mean squares for cross-fertility are presented in Table 18. Differences among entries were highly significant. No difference in cross-fertility was observed in the overall comparisons of crosses between and crosses within varieties. Among crosses between varieties, group I (Alfa X Vernal) showed higher cross-fertility than group II (Alfa X Kuban) and group III (Vernal X Kuban). Among crosses within varieties, group IV (Alfa X Alfa) and group V (Vernal X Vernal) showed significantly higher cross-fertility than group VI (Kuban X Kuban). Group V (Vernal X Vernal) exhibited higher cross-fertility than group IV (Alfa X Alfa).

Table 18. Analysis of variance mean squares for cross-fertility

Source of variation	D.F.	Mean squares
Entries	5	8.1239**
I,II,III vs. IV,V,VI	1	1.7763
I vs. II,III	1	14.5047**
II vs. III	1	0.0230
IV,V vs. VI	1	18.6756**
IV vs. V	1	5.6400**
Error	24	1.4504

DISCUSSION

Heterosis from outcrossing in alfalfa has been realized. Westgate (1910) and Waldron (1920) found that the F_1 hybrids from the cross *Medicago falcata* X *M. sativa* performed better than both parents. The increase in weight per plant over the parental plants was 47.5 percent (Waldron, 1920). A marked increase in forage yield of the F_1 hybrids over that of the parental lines was also reported by Tysdal, *et al.* (1942), Tysdal and Kiesselback (1944), and Wilsie (1958). From crosses involving erect and prostrate clones, Wilsie found a striking degree of heterosis with the F_1 hybrids, yielding 81 percent and 43 percent, respectively, above the higher yielding parent.

An important comparison in the present study was the performance of crosses between varieties and crosses within varieties. The three varieties used, Alfa, Vernal and Kuban, were unrelated and differed greatly in morphological characteristics. Alfa and Vernal are of *Medicago sativa* while Kuban is of *M. falcata*. The degree of diversity between varieties of different species should be greater than that of the same species. Therefore, interspecific crosses (Alfa X Kuban and Vernal X Kuban) are expected to exhibit more hybrid vigor than intraspecific crosses (Alfa X Vernal). Also, on the same basis, crosses between varieties (A X V, A X K and V X K) should outperform crosses within varieties (A X A, V X V and K X K). Hagberg (1952) found that the degree of heterosis in rye paralleled the degree of genetical differentiation between the populations crossed. In alfalfa, Lubenec (1959) found that inter-varietal and interspecific hybrids outyielded the local varieties. Results from the present study seem to agree well with these previous findings. In the first cutting of each year, crosses between varieties (A X V, A X K and V X K) outyielded crosses within varieties as well as check varieties. Interspecific crosses (Alfa X Kuban and Vernal X Kuban) outyielded intraspecific crosses (Alfa X Vernal). In the second cutting, however, the yield increase of crosses between varieties over that of crosses within varieties was small compared to the first cutting. This may be attributed to the slow rate of recovery after cutting of interspecific hybrids. Since the variety Kuban, M. falcata, has a very slow rate of recovery after cutting (Oakley and Garver, 1917), the second cutting yield of this variety and the yields of crosses within the variety, were very low. The characteristic slow rate of recovery after cutting may be transferred to the interspecific hybrids causing low yield in the second cutting. However, if the developmental period is extended, these interspecific hybrids might yield as well as intraspecific hybrids in the second cutting. Results from the second cutting of the second year tend to substantiate this hypothesis. Upon extending the harvesting date, no difference in yield was found between interspecific crosses and intraspecific crosses.

Crosses within varieties gave no yield advantage over the parental check varieties, in some case even less. Parental plants used in intravariety crosses were random plants from an open-pollinated population. Progenies obtained from crosses within such a population are expected to yield approximately the same as that of the open-pollinated variety, because no new germ plasm is added. In the present study in only one case (second cutting of the first year) was the difference in forage yield between crosses within varieties and check varieties significant (.05 level). In the first cutting of the first year, the forage yield of crosses within varieties was less than that of the check varieties, though the difference was not significant. This situation might be attributed to sampling error.

In comparison among crosses within varieties, the crosses Vernal X Vernal gave higher yields than the crosses Alfa X Alfa. This might be due to the high yielding ability of the variety Vernal itself and the high degree of diversity represented by its ancestral components. Among check varieties, Vernal gave the highest yield in all cases except in the first cutting of the first year when Kuban was the highest yielding variety. The crosses Kuban X Kuban gave the lowest yield among the crosses within varieties in all cases except in the first cutting of the first year. It has been found that in the first cutting Kuban usually gives as much yield as the varieties of _Medicago sativa_, in some cases even greater (Oakley and Garver, 1917). The serious drawback of this variety is in its inability to recover quickly after cutting. Moreover, Kuban suffered more from diseases and winter killing than other varieties in the present study.

Through hybridization, increased variation within populations is expected. The structure of the population from which the crosses are made is important in this respect. In the present study the varieties used in crossing differ in genetic base, Alfa being rather narrow and Vernal extremely broad (Bolton, 1962). The crosses involving Vernal, therefore would be expected to increase variability within the hybrid population.

In forage yield, the greatest variation was found within the crosses Vernal X Kuban. The variation within the crosses Alfa X Vernal was also found greater than that within the crosses Alfa X Kuban. In the first cutting of the first year, the mean yield of the crosses Vernal X Kuban ranged from 0.48 to 1.71, the crosses Alfa X Vernal from 0.57 to 1.18 and the crosses Alfa X Kuban from 1.01 to 1.35 (Table 19 in the Appendix). Among crosses within varieties, the crosses Vernal X Vernal showed greater variation (mean yields from 0.76 to 1.63) than the crosses Alfa X Alfa (mean yields from 0.42 to 0.92).

Most of the previous studies showed that both general and specific combining ability are important in alfalfa. Breeding methods designed to take advantage of both general and specific combining ability have been suggested. However, the relative importance of general and specific combining ability depends on breeding material used. Carnahan, et al., (1959) found that general combining ability was more important than specific combining ability when the clones used had not been selected previously for the traits studied. In the present study, three unrelated varieties were used. As expected, general combining ability was more important than specific combining ability in most instances. The reverse situation for forage yield in the second year possibly may be attributed to natural selection. The plants in the field in the second year were those that survived the effects of both winter injury and diseases. Moreover, late harvesting in the second year allowed the interspecific hybrids to reach their full development. These factors may cause more variability among groups of hybrids, and consequently a greater sum of squares among groups. Since general combining ability should be about the same for both years, residual effect then should be greater in the second year. This may cause the increase of specific combining ability mean squares.

The magnitude of forage yield in F_2 progenies was similar to that in F_1. Crosses between varieties (A X V, A X K and V X K) outyielded crosses within varieties (A X A, V X V, K X K). Instead of the crosses Vernal X Kuban being the highest yielding variety as was the case in F_1, the crosses Alfa X Kuban gave the highest yield. Since Vernal has a broader genetic base than Alfa, more segregation in F_2 generation is expected from the crosses Vernal X Kuban, and possibly this may account for the lower yield, on average, than that of the F_2 progenies of Alfa X Kuban. Considering variation within each group of crosses, crosses between varieties showed greater variation than crosses within varieties. There is no appropriate way to compare statistically the performance of F_1 and F_2 in this study. One aspect, however, that of their variability, can be compared. Significant mean squares within each group of crosses were found more often in F_1 than in F_2. This may be expected since the parental plants used were highly heterozygous. The variability in each group of crosses should decrease in advanced generation of selfing. Selection made in F_1 would be more effective.

Estimating the percent crossed seed a given alfalfa genotype will produce in the field is of importance to those using polycross or single cross methods in alfalfa breeding (Gartner and Davis, 1966). High seed yield together with a high percentage of outcrossing is desirable for clones entering synthetic varieties or two clone crosses. Tysdal, et al. (1942) proposed a breeding program using self-sterile clones for the production of hybrid alfalfa. Two completely self-sterile clones, that were cross-compatible, would produce an abundance of seed when crosses with each other. However, a recent study by Carleton and Eslick (1967) indicated that low self-compatibility of the female was associated with low cross seed set of that female. They concluded that selection of two clones sufficiently self-sterile to produce nearly all hybrids would result in very low seed set. Some degree of self-compatibility thus appears desirable in either one or both of the parental clones.

Medicago falcata has been found to cross readily with M. sativa (Sprague, 1956). These two species could be used in any combination in a breeding program without meiotic difficulties. However, in the present study the crosses between M. falcata and M. sativa showed lower cross-fertility than the crosses within M. sativa. When M. falcata was used as the female parent, very little seed set was obtained. This might be attributed to the low self-compatibility in M. falcata. Similar result was found by Waldron (1919) who attributed this to the comparative scarcity of both flowers and pollen in M. falcata. More F_1 seeds were obtained when M. sativa was used as the female parent. Some of these F_1 seeds, however, might be selfed seeds. Using the criterion that the F_1 hybrids between M. falcata and M. sativa should produce variegated flowers, 85.5 percent of the plants in the F_1 progenies in the field probably were hybrid plants. This percentage of hybrids is low compared with that obtained in some previous studies. Carnahan (1963), in his study of a 6-clone diallel, stated that crossing among unrelated plants, even without emasculation, resulted in few selfed seeds. Also, Tysdal, et al. (1942) reported an average of 89.1 percent cross-pollination based on the use of yellow and white flowers as testers. Recently Carleton and Eslick (1967) found that a high self-compatibility clone and a medium self-compatibility clone had average percentages of crossed seed of 45 and 35, respectively, when crossed with nonemasculated white-flowered female clone.

In the present study self-fertility of parental plants, especially that of Kuban variety was quite low. Since a fairly high degree of self-compatibility is desirable in parental clones entering synthetic varieties or two clone crosses (Carleton and Eslick, 1967), improving self-fertility in these parental plants might be useful. One way to do this is to make crosses between these plants. Unless the parents are extremely high in self-fertility, it is expected that their hybrids will have higher self-fertility. Results from the present study agree with this expectation. All F_1 hybrids had higher self-fertility than either of their parents.

SUMMARY AND CONCLUSIONS

A study was undertaken to determine what kind of parental plants or populations should be used in crossing in order to capitalize on maximum hybrid vigor. Twenty random plants from each of three alfalfa varieties were used in intra- and intervariety crosses. Agronomic characteristics in F_1 and F_2 progenies were studied.

1. In general, intervariety crosses outperformed intravariety crosses. Intervariety crosses outyielded the parental check varieties while intravariety crosses did not. Among intervariety crosses, interspecific crosses, on average, outyielded intraspecific crosses. The crosses within variety Vernal showed the highest yield among intravariety crosses, though the yield was not significantly different from that of check varieties. The diversity of parent plants and broad genetic base population were found important in obtaining hybrid vigor.

2. Hybridization is a means in creating variability in plant populations. The crosses that involved a population of broad genetic base exhibited greater variation than those that involved a population of narrow base.

3. The alfalfa varieties used in the present study were unrelated. As expected, general combining ability was more important than specific combining ability in most instances.

4. The performance of F_2 progenies was similar to that of F_1. Intervariety crosses outperformed intravariety crosses. However, variability in F_2 appeared to be less than that in F_1 which suggests that selection in

F_1 might be more effective than in F_2.

5. Cross-fertility of intravariety crosses was higher than that of intervariety crosses. The highest cross-fertility was found in the crosses Vernal X Vernal and lowest in the crosses Kuban X Kuban.

6. In the material studied, self-fertility of F_1 progenies was found greater than that of either parent involved.

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APPENDIX

Table 19. Performance of the F_1 progenies for agronomic characteristics

Entry	Yield, 1st cutting	1966 2nd cutting	Yield, 1st cutting	1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Rate of recovery
1	1.11	0.59	1.20	0.84	1.6	2.8	3.5	1.7
2	0.66	0.41	0.72	0.54	2.1	4.1	4.9	3.0
3	0.98	0.57	1.05	0.66	2.3	3.4	4.4	2.2
4	0.72	0.48	0.79	0.63	3.6	4.5	4.4	3.4
5	1.18	0.62	1.45	0.96	2.8	2.4	2.2	1.7
6	1.05	0.62	1.43	0.92	2.4	3.1	1.9	1.6
7	0.85	0.49	1.04	0.69	3.7	3.8	3.6	2.4
8	0.66	0.46	0.82	0.72	3.0	3.6	4.2	1.7
9	0.77	0.50	1.14	0.75	2.3	4.0	3.3	2.5
10	0.57	0.38	0.75	0.61	3.3	4.3	4.7	2.2
11	1.22	0.40	1.43	0.59	2.8	3.3	3.6	4.2
12	1.21	0.39	1.66	0.66	2.8	3.2	3.0	3.4
13	1.01	0.37	1.05	0.49	3.3	3.8	3.9	3.7
14	1.02	0.34	1.22	0.52	2.8	4.2	4.1	3.9
15	1.22	0.54	1.56	0.94	2.3	1.9	1.4	1.6
16	1.21	0.51	1.57	1.01	2.4	2.1	1.9	1.5
17	1.35	0.42	1.57	0.67	2.9	3.8	2.9	3.2
18	0.95	0.39	1.36	0.61	4.0	4.5	4.0	2.3
19	0.48	0.25	0.57	0.52	6.1	7.1	6.2	4.7
20	1.29	0.45	1.55	0.69	3.1	3.4	2.4	2.4
21	1.13	0.35	1.21	0.57	4.1	3.9	3.7	4.9
22	1.85	0.60	1.93	0.82	2.4	1.8	1.7	2.5
23	1.33	0.58	1.72	0.95	3.2	2.7	1.9	1.9
24	1.71	0.71	2.07	0.96	2.7	2.1	1.9	2.0
25	0.66	0.41	0.69	0.45	2.4	4.3	5.0	3.0
26	0.61	0.47	0.66	0.62	2.1	4.6	5.0	2.7
27	0.80	0.49	0.87	0.67	2.1	4.0	4.4	1.8

Table 19. (Continued)

Entry	1966 Yield, 1st cutting	1966 2nd cutting	1967 Yield, 1st cutting	1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Rate of recovery
28	0.76	0.52	0.80	0.77	2.2	4.0	4.4	2.0
29	0.92	0.53	0.91	0.65	1.7	3.0	4.3	2.2
30	0.57	0.35	0.75	0.60	2.6	4.7	4.5	3.4
31	0.82	0.55	0.95	0.62	2.1	3.7	3.6	2.1
32	0.58	0.39	0.63	0.60	2.6	4.2	4.7	2.4
33	0.42	0.29	0.65	0.48	2.3	6.0	5.4	3.3
34	0.57	0.39	0.76	0.56	3.3	4.9	5.0	1.4
35	0.86	0.56	1.19	0.92	3.3	3.1	2.9	1.4
36	0.92	0.49	0.91	0.70	2.7	3.5	3.6	1.5
37	0.78	0.49	1.08	0.79	2.7	4.4	3.6	1.8
38	0.77	0.52	1.06	0.75	4.3	4.3	3.2	2.3
39	0.76	0.45	0.86	0.71	2.1	4.0	3.2	1.9
40	0.92	0.46	0.93	0.72	2.9	3.6	3.7	2.7
41	0.88	0.52	1.10	0.75	2.3	3.3	3.4	2.2
42	0.81	0.53	1.00	0.82	2.6	3.3	3.8	1.7
43	0.91	0.41	0.98	0.65	3.2	3.6	4.4	3.3
44	1.63	0.30	0.83	0.58	3.9	4.9	4.4	2.7
45	0.93	0.08	0.45	0.09	7.0	5.4	7.2	8.5
46	1.08	0.11	0.13	0.13	6.2	4.0	6.0	8.2
47	0.77	0.04	0.60	0.06	7.6	5.9	8.5	8.6
48	1.01	0.13	0.64	0.13	6.8	4.8	5.9	8.2
49	0.94	0.09	0.46	0.11	6.4	5.2	6.2	8.4
50	1.00	0.05	0.39	0.09	7.0	4.3	7.3	8.9
51	1.04	0.08	0.54	0.12	6.3	4.4	6.7	8.5
52	1.38	0.39	1.20	0.55	2.7	2.7	3.6	4.5
53	0.81	0.06	0.30	0.08	6.4	5.3	7.7	8.4
54	0.55	0.37	0.68	0.54	2.4	5.1	5.4	8.4

Table 19. (Continued)

Entry	Yield, 1st cutting	1966 2nd cutting	Yield, 1st cutting	1967 2nd cutting	Seedling vigor 1965	Spring vigor 1966	Spring vigor 1967	Rate of recovery
55	0.88	0.42	1.01	0.68	3.6	4.1	4.4	3.5
56	1.23	0.10	0.59	0.13	5.2	4.3	6.7	8.3

Entry	Plant height 1965	1966	Plant width 1965	1966	Flower color	Winter killed	Winter injury	Disease killed	Persistence
1	45.8	55.5	48.1	45.1	2.2	1.0	1.0	1.0	1.0
2	44.0	51.6	44.2	37.1	2.1	1.0	1.0	1.0	1.5
3	39.6	53.2	49.3	42.9	2.2	1.0	1.0	1.0	1.0
4	38.8	51.2	52.8	47.1	2.6	1.0	1.5	1.0	1.0
5	39.0	54.2	51.7	45.4	3.1	2.0	1.0	1.0	2.0
6	45.2	54.6	52.2	48.4	1.5	1.0	2.0	3.0	3.0
7	37.9	50.1	47.7	36.6	2.8	2.0	1.0	1.0	2.0
8	34.1	50.5	38.6	39.4	3.0	1.5	1.0	1.0	1.5
9	38.2	48.6	51.1	43.1	2.3	2.5	1.0	1.0	2.5
10	42.2	51.4	34.1	33.9	2.2	2.5	1.0	1.0	3.0
11	38.6	37.4	47.4	42.7	4.1	1.5	1.0	1.0	2.0
12	36.7	36.1	47.7	41.1	1.5	1.5	1.0	2.0	2.0
13	34.5	40.7	44.4	40.8	3.4	1.0	1.0	1.5	2.0
14	36.5	34.6	41.4	39.4	4.1	2.0	1.0	1.0	2.5
15	37.3	48.9	43.1	44.4	3.9	1.5	1.0	1.0	1.5
16	34.8	48.1	43.1	41.8	3.9	1.0	1.0	1.0	1.0
17	39.1	37.7	50.6	44.9	4.5	1.9	1.0	1.0	1.5
18	33.5	42.3	46.2	37.5	3.6	2.2	1.0	1.0	2.2

Table 19. (Continued)

Entry	Plant height 1965	Plant height 1966	Plant width 1965	Plant width 1966	Flower color	Winter killed	Winter injury	Disease killed	Persistence
19	28.5	38.9	32.7	34.1	2.7	0.9	1.1	4.0	4.0
20	30.7	41.1	56.5	41.9	4.3	1.0	1.5	1.0	1.5
21	27.9	33.4	51.1	35.1	4.5	1.9	1.7	2.1	3.0
22	30.9	44.7	62.3	46.2	4.6	2.0	1.0	1.0	3.0
23	35.7	49.9	51.9	43.1	1.5	1.0	1.0	1.0	1.5
24	33.0	46.6	68.9	57.6	3.9	1.5	1.0	1.0	1.5
25	46.0	53.7	40.0	32.0	2.1	2.0	2.0	1.5	3.5
26	46.5	55.8	42.5	35.9	2.6	3.5	1.0	1.0	4.5
27	46.1	54.6	50.6	41.2	2.7	1.5	1.0	1.0	2.0
28	40.8	54.2	43.0	42.4	2.2	1.5	1.0	1.0	2.0
29	48.5	59.5	44.2	42.2	2.2	1.0	1.0	1.0	1.5
30	38.9	48.9	33.1	32.5	2.3	2.5	1.0	1.0	2.5
31	48.1	57.2	44.8	39.2	2.3	1.0	1.0	1.5	2.0
32	41.1	55.4	35.4	38.3	2.2	1.5	1.5	1.0	2.0
33	41.9	48.7	29.0	28.0	2.2	1.0	2.0	1.5	2.0
34	41.9	50.1	39.9	33.6	2.2	2.5	1.5	1.0	3.5
35	33.4	53.0	45.1	45.5	2.2	1.0	1.0	1.0	1.0
36	39.8	50.6	43.8	45.0	2.2	1.0	1.0	1.0	1.0
37	39.4	50.7	39.8	41.1	2.3	1.0	1.0	1.0	1.0
38	29.3	50.0	50.8	51.9	3.3	1.0	1.0	1.0	1.0
39	40.1	51.7	44.6	38.9	3.3	1.0	1.0	1.0	1.0
40	39.4	53.4	54.1	46.4	3.4	1.0	1.0	1.0	1.5
41	36.4	50.5	57.5	43.7	2.6	1.0	1.0	1.0	1.0
42	38.2	52.5	47.3	46.6	3.1	1.0	1.0	1.0	1.0
43	37.2	49.0	46.7	38.8	2.2	1.0	1.0	1.0	1.0
44	36.4	44.3	37.0	35.8	2.2	1.0	1.0	1.0	1.0
45	22.5	18.0	62.7	28.2	5.3	2.0	1.5	1.5	6.0

Table 19. (Continued)

Entry	Plant height 1965	Plant height 1966	Plant width 1965	Plant width 1966	Flower color	Winter killed	Winter injury	Disease killed	Persistence
46	20.8	18.1	62.7	32.1	5.3	1.0	1.0	1.0	1.0
47	16.0	16.8	58.4	21.4	5.3	2.0	2.5	3.5	9.0
48	16.2	23.6	54.3	32.7	5.3	1.0	1.0	1.0	1.5
49	25.9	24.7	50.6	24.8	5.3	1.0	1.5	1.5	2.5
50	20.9	20.6	52.5	24.0	5.3	2.0	1.5	3.5	6.0
51	22.4	19.2	59.7	26.2	5.3	2.0	2.0	2.0	6.0
52	32.0	41.8	53.4	39.7	4.1	0.9	1.0	1.0	0.9
53	22.5	17.1	49.0	20.2	5.3	1.5	1.0	1.5	4.5
54	41.7	51.4	41.5	44.5	2.2	1.0	1.0	1.0	1.0
55	32.6	44.7	43.6	40.2	3.0	1.5	1.5	1.0	2.5
56	22.5	19.8	68.4	28.1	5.2	2.0	1.0	1.5	6.0

Table 20. Performance of the F_2 progenies for agronomic characteristics

Entry	Yield		Seedling vigor	Spring vigor	Rate of recovery
	1st cutting	2nd cutting			
1	1.29	0.37	1.9	1.9	3.3
2	0.72	0.30	2.6	3.8	4.1
3	0.82	0.41	2.4	2.2	1.8
4	1.20	0.48	1.6	2.7	1.9
5	1.33	0.59	3.5	2.2	1.3
6	0.86	0.42	2.5	3.0	2.2
7	0.74	0.37	2.4	3.4	2.7
8	1.65	0.44	1.7	1.6	3.0
9	1.61	0.39	1.6	1.4	3.2
10	1.47	0.53	1.5	1.3	1.6
11	1.02	0.39	3.4	1.8	2.2
12	0.45	0.22	4.3	5.8	5.1
13	0.63	0.32	3.3	3.9	2.2
14	0.57	0.25	3.9	4.3	3.6
15	1.43	0.41	2.5	1.8	3.1
16	1.47	0.34	2.9	1.9	4.8
17	1.45	0.45	2.0	1.2	1.7
18	0.47	0.20	2.7	5.1	5.1
19	0.57	0.30	3.9	4.7	3.1
20	0.63	0.28	2.9	4.9	3.6
21	0.50	0.29	3.5	4.9	4.4
22	0.73	0.31	3.5	4.3	2.3
23	0.69	0.29	3.7	3.5	2.6
24	0.57	0.21	4.6	3.9	4.2
25	0.74	0.30	3.2	4.2	2.9
26	0.67	0.25	3.7	3.8	3.2
27	0.67	0.26	3.4	4.6	3.6
28	0.76	0.29	4.3	4.0	3.8
29	0.67	0.28	3.1	2.8	2.5
30	0.76	0.29	2.6	4.0	4.7
31	0.79	0.29	3.3	3.6	2.9
32	0.94	0.28	2.5	2.7	4.2
33	0.64	0.27	3.5	4.2	3.1
34	0.75	0.38	3.0	3.6	2.4
35	1.32	0.52	3.7	2.1	2.0
36	1.72	0.16	2.8	2.1	8.7

Table 21. Self- and cross-fertility indices

Entry	Cross	Self-fertility index	Cross-fertility index	Entry	Parent plant	Self-fertility index
1	A_4 X V_4	2.54	2.86	31	A_4	0.22
2	A_5 X V_5	2.02	5.28	32	A_5	0.44
3	A_7 X V_7	1.27	5.34	33	A_7	1.36
4	A_8 X V_8	0.58	2.80	34	A_8	0.48
5	A_9 X V_9	0.81	2.76	35	A_9	0.50
6	A_4 X K_4	1.02	0.41	36	A_{14}	1.08
7	A_5 X K_5	0.71	0.49	37	A_{15}	0.39
8	A_7 X K_7	1.23	1.71	38	A_{17}	0.13
9	A_8 X K_8	0.33	3.98	39	A_{18}	0.00
10	A_9 X K_9	0.51	1.78	40	A_{19}	0.34
11	V_4 X K_4	0.98	0.64	41	V_4	2.58
12	V_5 X K_5	0.03	0.51	42	V_5	1.84
13	V_7 X K_7	2.16	2.02	43	V_7	1.77
14	V_8 X K_8	1.59	3.09	44	V_8	1.77
15	V_9 X K_9	0.17	2.59	45	V_9	0.71
16	A_4 X A_{14}	0.84	3.73	46	V_{14}	0.06
17	A_5 X A_{15}	0.89	4.27	47	V_{15}	0.16
18	A_7 X A_{17}	1.36	4.19	48	V_{17}	0.77
19	A_8 X A_{18}	0.94	1.43	49	V_{18}	0.21

Table 21. (Continued)

Entry	Cross	Self-fertility index	Cross-fertility index	Entry	Parent plant	Self-fertility index
20	A_9 X A_{19}	0.56	1.09	50	V_{19}	0.31
21	V_4 X V_{14}	2.82	4.19	51	K_4	0.00
22	V_5 X V_{15}	0.56	4.00	52	K_5	0.00
23	V_7 X V_{17}	0.95	4.22	53	K_7	0.11
24	V_8 X V_{18}	1.04	4.05	54	K_8	0.46
25	V_9 X V_{19}	1.84	5.76	55	K_{10}	0.00
26	K_4 X K_{14}	0.00	0.86	56	K_{14}	0.57
27	K_5 X K_{15}	0.37	1.61	57	K_{15}	0.00
28	K_7 X K_{17}	0.00	1.57	58	K_{17}	0.02
29	K_8 X K_{18}	1.62	0.46	59	K_{18}	0.00
30	K_{10} X K_{20}	0.00	2.13	60	K_{20}	0.00

Table 22. Barnes' proposed scale for visually scoring alfalfa flower color

Numerical rating	Primary flower color	Secondary flower color	Probable genotype
1	White		cccc P--- yyyy cccc pppp yyyy
2	Purple, violet or lilac		C--- P--- yyyy
2.1		Dark	
2.2		Moderately dark	
2.3		Light	
2.4		Very light	
3	Cream		C--- pppp yyyy cccc P--- Y--- cccc pppp Y---
4	Variegated		C--- P--- Y---
4.0		Purple variegated-dark	
4.1		Purple variegated-light	
4.2		Blue-dark	
4.3		Blue-light	
4.4		Maroon-dark	
4.5		Maroon-light	
4.6		Green-dark	
4.7		Green-light	
4.8		Yellow variegated-dark	
4.9		Yellow variegated-light	
5	Yellow		
5.1		Very light	
5.2		Light	
5.3		Moderately dark	
5.4		Orange	